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**Title**

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**Permalink**

<https://escholarship.org/uc/item/49m7k73c>

**Journal**

Arctic, Antarctic, and Alpine Research, 46(2)

**ISSN**

1523-0430

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**Publication Date**

2014-05-01

**DOI**

10.1657/1938-4246-46.2.355

Peer reviewed

# Hydrological Control of Greenhouse Gas Fluxes in a Sierra Nevada Subalpine Meadow

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## Abstract

Alpine and subalpine meadows are often hotspots of water availability and biodiversity in montane landscapes, but we know little about whether these attributes also make meadows hotspots of greenhouse gas (GHG) emission. Furthermore, many of these meadows will likely become drier during the growing season in the future because of less precipitation, earlier timing of snowmelt, and increased evapotranspiration associated with climatic warming. To evaluate the potential effects of soil drying on GHG emission, we studied a soil moisture gradient in a Sierra Nevada subalpine meadow in California. Our objectives were: (1) to assess the strength of hydrological control for soil carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxide (N<sub>2</sub>O) fluxes both earlier and later in the growing season; and (2) to quantify the contribution of CH<sub>4</sub> and N<sub>2</sub>O to net GHG emission. The replicated gradient spanned 50 m, from the wet middle to dry edge of the meadow, and soil volumetric water content was measured 0 to 12 cm deep. Fluxes of CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O were measured using static chambers at 10 m intervals across the gradient. We found that the wet side of the gradient was not a CH<sub>4</sub> or N<sub>2</sub>O source on either sampling date. Net CH<sub>4</sub> emission from soil was rare and CH<sub>4</sub> uptake was prevalent, particularly on the dry side of the gradient. Soil N<sub>2</sub>O fluxes shifted from net uptake at the middle of the meadow to net emission at the edge, but only earlier in the growing season. Of the three GHGs, CO<sub>2</sub> fluxes showed the most temporal variation but surprisingly varied little across the hydrological gradient. Other environmental factors—including plant species richness and soil carbon concentration—appeared more important than soil moisture in explaining CO<sub>2</sub> fluxes. Therefore, the strength of near-surface hydrological control increased in the following order: CO<sub>2</sub> < N<sub>2</sub>O < CH<sub>4</sub>. Our results suggest that non-CO<sub>2</sub> greenhouse gases will need proper accounting during the snow-free season in order to more accurately predict the effects of future soil drying on GHG emissions in heterogeneous montane landscapes.

DOI: <http://dx.doi.org/10.1657/1938-4246-46.2.355>

## Introduction

Greenhouse gas (GHG) emissions from terrestrial ecosystems—which influence the global heat balance of the planet—often reflect changes in water availability across the landscape (Smith et al., 2003). Wet montane meadows, for example, can emit more carbon dioxide (CO<sub>2</sub>) than surrounding drier upland forests (Riveros-Iregui and McGlynn, 2009). Wet montane meadows store carbon through high rates of plant production during the growing season followed by an extended cold season with low rates of microbial decomposition (Kato et al., 2004, 2006; Hu et al., 2010). Despite their relatively small area (e.g., 3% of Sierra Nevada in California; Keeler-Wolf et al., 2012), meadows could be significant sources of CO<sub>2</sub>, methane (CH<sub>4</sub>), and nitrous oxide (N<sub>2</sub>O) because of high organic matter content and relatively low water limitation during the snow-free period (i.e., subsurface water sources and high field capacities due to high organic matter content). Many high-elevation ecosystems are likely on the cusp of hydrological and biogeochemical changes resulting from less precipitation (Seager et al., 2007), earlier timing of snowmelt (Mote et al., 2005; Stewart et al., 2005), and increased evapotranspiration due to climatic warming (Harte et al., 1995; Barnett et al., 2005; Fu et al., 2012). By better understanding current hydrological controls of GHG fluxes in high-elevation meadows, we can more accurately predict the effects of future soil drying on GHG emissions in heterogeneous montane landscapes.

Predicting the magnitude of CO<sub>2</sub> emission and the direction of CH<sub>4</sub> and N<sub>2</sub>O fluxes in montane meadows is not straightforward. Most studies do not measure all three major GHGs together at the same site. Thus, it remains unclear how soil moisture in montane meadows influences the relative contribution of non-CO<sub>2</sub> GHGs to net radiative forcing (Jiang et al., 2010). Soil CH<sub>4</sub> and N<sub>2</sub>O fluxes vary from net production to net consumption, depending on soil moisture, oxygen concentration, temperature, pH, nitrogen content, and microbial community structure (Mosier et al., 1993; Torn and Harte, 1996; Filippa et al., 2009; Lin et al., 2009; Hu et al., 2010; Jiang et al., 2010; Giles et al., 2012). By not accounting for CH<sub>4</sub> and N<sub>2</sub>O—which have much higher warming potentials per mole than CO<sub>2</sub>—we could be ignoring an important component of the GHG budget of montane meadows.

We may also be ignoring GHG-specific responses to drying. Can we assume, for example, that areas with dry surface soil also emit less CO<sub>2</sub>? And does wet surface soil necessarily express net CH<sub>4</sub> emission? Meadow CO<sub>2</sub> fluxes often show large spatial variation and can be limited by too little water, too much water (i.e., slower anaerobic metabolism and reduced diffusional transport from deep soil), cold temperatures, and availability of labile carbon (Fisk et al., 1998; Saleska et al., 1999; Kato et al., 2004; Pacific et al., 2008, 2009; Saito et al., 2009; Suh et al., 2009; Jiang et al., 2010). There is also evidence that plant root respiration (as estimated by root biomass) can be more important than microcli-

mate in explaining meadow CO<sub>2</sub> fluxes (Geng et al., 2012). Plant cover and diversity may also affect CH<sub>4</sub> and N<sub>2</sub>O fluxes by altering carbon and nitrogen availability (Niklaus et al., 2006). Net CH<sub>4</sub> emission is favored in wetter soils (Mosier et al., 1993; Whalen, 2005), but the extent of CH<sub>4</sub> consumption in drier meadow soils is unclear. Net N<sub>2</sub>O emission can also relate positively to soil moisture (Mosier et al., 1993; Fisk et al., 1998; Filippa et al., 2009) or show no relation to commonly measured environmental variables (Jiang et al., 2010). Thus, the controls on each GHG are apparently different, but because multiple GHGs have not been studied at many sites, we do not know how broadly these controls apply.

A hydrological gradient based on meadow topography is a way to assess the relative control of soil moisture on GHG fluxes. Topographic position relates to soil moisture, which may in turn relate to GHG fluxes, which thus aids in the modeling and upscaling of GHG emissions across montane landscapes (Fisk et al., 1998; Grayson and Western, 1998; Western et al., 1999; Riveros-Iregui and McGlynn, 2009; Pacific et al., 2011; Jeong et al., 2012). The depth of the groundwater table typically decreases from the middle to edges of meadows (Lowry et al., 2010), resulting in drier soils near the edges. Greenhouse gas emissions are expected to follow a similar pattern (Mosier et al., 1993)—decreasing from the middle to the edges—but few studies have attempted to quantify this spatial pattern.

The Sierra Nevada in California provides an ideal alpine setting to investigate hydrological control of meadow GHG fluxes during the growing season because of the abundance of montane meadows and the Mediterranean-type climate. Sierra Nevada meadows, as opposed to the Rocky Mountains for example, receive almost no precipitation after spring snowmelt and are therefore expected to provide a consistent topographic soil moisture gradient without the confounding effects of summer precipitation. Soil moisture can strongly control CO<sub>2</sub> emission in a Mediterranean-type climate (Correia et al., 2012), but, to date, no study has measured all three major GHGs simultaneously within the same Sierra Nevada meadow. A spring-fed wetland in the Sierra Nevada foothills was found to be a hotspot of CH<sub>4</sub> and N<sub>2</sub>O emission compared to surrounding oak savanna (Oates et al., 2008). We therefore expected that the wetter portion of a subalpine meadow would also be a hotspot of CH<sub>4</sub> and N<sub>2</sub>O emission.

We measured GHG fluxes across a soil moisture gradient from the middle to edge of a Sierra Nevada subalpine meadow in Yosemite National Park. To determine whether the effect of seasonal drying is similar to the effect of drying along the hydrological gradient, we measured GHG gas fluxes both earlier and later in the growing season. The gradient spanned from wet soils near field capacity at the middle of the meadow to considerably drier soils at the edge of the meadow. To identify the potential impacts of future soil drying, our first objective was to quantify the strength of hydrological control on different GHG fluxes. We hypothesized that the wetter portion of the meadow would be a hotspot of GHG emission compared to the drier edge. Our second objective was to determine the contribution of CH<sub>4</sub> and N<sub>2</sub>O fluxes to net GHG emission in a subalpine meadow. We expected that CH<sub>4</sub> and N<sub>2</sub>O fluxes would contribute most to net GHG emission in the wetter portion of the meadow.

## Methods

### SITE DESCRIPTION

A Sierra Nevada subalpine meadow (2860 m a.s.l.; 37.8997°N, 119.3397°W) was chosen based on trail access (~5 km north-northeast of Tuolumne Meadows in Yosemite National

Park, California, U.S.A.) and minimal previous disturbance (i.e., no recreational camping or packstock use). The sampled portion of the meadow was at least 200 m from the trail and showed no signs of human disturbance. The middle of the meadow was slightly lower in elevation, surrounded by a higher and drier edge of the meadow that transitioned to coniferous forest approximately 50 m beyond where we sampled. The meadow was oriented east-west (slope < 5°) with Delaney Creek near the middle flowing west. The meadow was medium-sized (15.8 ha) compared to other meadows in Yosemite National Park, and dominated by small-statured plant species (<30 cm tall) including *Aster alpigenus*, *Calamagrostis breweri*, *Carex filifolia*, *Deschampsia cespitosa*, and *Vaccinium caespitosum*.

A weather station at Ellery Lake, California (WRCC, 2009), located 10 km northeast of the meadow at a similar elevation (2907 m a.s.l.), approximated the climate at our site. This area experiences a Mediterranean-type climate with less than 5% of annual precipitation falling during summer. The growing season lasts approximately 3 months (July until September), during which the groundwater table can fall from above the soil surface to more than 1.5 m below the soil surface (Lowry et al., 2010). The mean annual precipitation is 63.7 cm of water equivalent, with a mean annual cumulative snowfall of 544 cm. The mean maximum monthly snow depth (150 cm) typically occurs in March. The mean maximum air temperature in July is 19.8 °C, and the mean minimum air temperature in January is −11.8 °C (mean annual air temperature is ~3 °C). The mean air temperature in July and September, the months sampled, is 12.2 °C and 8.3 °C, respectively.

Soils within the meadow are classified as the Marmotland–Oxyaquic Dystrocrepts–Xeric Dystrocrepts complex. Marmotland, the dominant soil within the meadow (25%), is classified within the coarse-loamy, isotic, Vitrandic Dystrocrepts Soil Taxonomic family. The Marmotland soil series consists of very deep, moderately well drained or well drained soils that formed in alluvium or minor till derived from granitoid rock and volcanic ash. Occasionally, an organic litter layer (Oi, <1 cm thick) overlaid the mineral soil. The surficial mineral soil horizon (A1, 0–29 cm) has a fine sandy loam texture and is strongly acid (pH 5.1; USDA NRCS, 2007).

### HYDROLOGICAL GRADIENT LAYOUT

The meadow was surveyed in mid-July 2010 (as soon as Tioga Pass Road opened) to identify a suitable area with unidirectional variation in soil moisture. A 50 × 70 m sampling grid was marked on the northern half of the meadow, spanning from the lower and wetter middle to the higher and drier edge. To capture the hydrological gradient, the 50 m side of the grid was oriented north-south, from the middle toward the edge at 10 m intervals. The 70 m side of the grid was oriented east-west marking the start of eight gradient transects spaced 10 m apart.

Soil volumetric water content (VWC) was measured immediately after gas flux sampling both early (28 July 2010) and late in the growing season (11 September 2010). Soil VWC was measured 5 cm to the south of each gas flux chamber and 0 to 12 cm below the soil surface using a portable time domain reflectometer (CD620 Hydrosense System, Campbell Scientific, Logan, Utah). The wet side of the gradient was near field capacity (~70% VWC) in July, which was approximately 3 weeks after snowmelt.

To assess non-moisture controls on GHG fluxes, we also measured midday soil temperature (both dates), plant species richness (July only), and soil chemistry (September only). Soil temperature was measured 5 cm to the south of each gas flux chamber and 6

cm below the soil surface (VWR Digital Dial Thermometer, VWR International, Radnor, Pennsylvania). Three temperature readings were recorded before, during, and after gas flux sampling, and then averaged. Plant species richness was measured to explain variation in gas fluxes potentially caused by differences in root respiration (presence/absence of plants) and resource utilization. Richness was determined by counting the number of different plant species present within the same 10.2-cm-diameter circular plots that were used to measure gas fluxes (0.0082 m<sup>2</sup>). If there was no above-ground plant growth in a plot, then species richness was recorded as zero. A species richness of three was the maximum that occurred with replication; there was one plot with a species richness of four. Soil chemical measurements are described separately below.

#### GAS FLUX SAMPLING

Field fluxes of carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxide (N<sub>2</sub>O) were measured between 13:00 and 17:00 on 28 July and 29 July 2010 (eight transects) and 11 September 2010 (four transects) using the static chamber technique (Hutchinson and Mosier, 1981; Hart, 2006). Every other transect was sampled in September because of logistical constraints; there were not enough people or daylight to sample all eight replicates during the same day.

Chamber tops were constructed from a 10.2-cm-diameter white PVC pipe closed at one end with a 4-cm-tall PVC cap equipped with a rubber septum and vent tube. The length (10 cm) and diameter (0.5 cm) of the vent tube were calculated to minimize chamber air mixing with outside air due to sample collection and perturbations from wind (i.e., the Venturi effect). Because of National Park Service regulations, the anchors for the chamber tops were not permanently installed at the site. Instead, to minimize artifacts of disturbance, the 14-cm-tall PVC anchors were inserted 4 cm into the soil at least 2 h before gas sampling began. Small flags were used to mark plot locations between sampling dates.

Headspace gas samples (18 mL) were collected from each chamber using a 20 mL polyethylene syringe with stopcock and 20-gauge needle. Gas samples were collected 0, 20, and 40 minutes after sealing the chamber top and applying a latex band as a secondary airtight seal between the chamber top and anchor. Gas samples were injected into 12 mL evacuated glass vials with rubber septa (Exetainer, Labco, Lampeter, Ceredigion, U.K.) until laboratory analysis (2 mL injection volume) on a gas chromatograph system (GC 2014 Greenhouse Gas Analyzer, Shimadzu Scientific Instruments, Columbia, Maryland) with Combi Pal AOC 5000 auto injector (CTC Analytics, Zwingen, Switzerland). The gas chromatograph used packed stainless steel columns (oven temperature = 80 °C) and was equipped with a flame ionization detector (FID) to measure CH<sub>4</sub> concentration, a thermal conductivity detector (TCD) to measure CO<sub>2</sub> concentration, and an electron capture detector (ECD) to measure N<sub>2</sub>O concentration. The FID and TCD were set at 250 °C and 150 °C, respectively, and equipped with Hayesep D 80/100, Hayesep T 80/100, and Shimalite Q 100/180 columns (3.2 mm diameter). The ECD was set at 325 °C and equipped with Hayesep D 80/100, Hayesep N 80/100, and Porapak N 80/100 columns (1.6 mm diameter).

In July, concentrations of CO<sub>2</sub> ranged from an average of 476 parts per million (ppm) at the start of flux measurements to 2847 ppm after 40 min (429–1299 ppm in September). The range of CH<sub>4</sub> concentrations was 2.2–1.7 ppm in July and 2.2–1.8 ppm in September. The range of N<sub>2</sub>O concentrations was 0.34–0.33 ppm in July and 0.45–0.43 ppm in September. Carbon dioxide and CH<sub>4</sub>

fluxes were linear during the 40-min sampling period (mean  $r^2$  = 0.99 and 0.97, respectively), and N<sub>2</sub>O fluxes were approximately linear (mean  $r^2$  = 0.54). It is possible that N<sub>2</sub>O was more sensitive than the other gases to the pressure perturbation of sealing the chamber top (Curiel Yuste et al., 2007), or the disturbance of installing the anchors 2 h prior. For the roughly one-third of chambers where N<sub>2</sub>O flux was clearly not linear, fitting with parabolic or exponential curves greatly improved the  $r^2$  value ( $\geq 0.95$ ) but did not improve our ability to determine an hourly N<sub>2</sub>O flux rate. To minimize error propagation caused by regression (particularly for N<sub>2</sub>O), we calculated the flux rate for all three gases by subtracting the known initial concentration from the known final concentration after 40 min. Net CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O fluxes were expressed as mg C m<sup>-2</sup> h<sup>-1</sup>,  $\mu$ g C m<sup>-2</sup> h<sup>-1</sup>, and  $\mu$ g N m<sup>-2</sup> h<sup>-1</sup>, respectively. Positive rates indicate net emission (from soil to atmosphere), and negative rates indicate net uptake (from atmosphere to soil).

#### LABORATORY SOIL CHEMICAL ANALYSES

Soil samples (0 to 12 cm) were collected from all eight transects immediately after gas sampling in September using an Oakfield soil probe (2 cm diameter). We did not collect soil in July to minimize potential disturbance effects on future gas flux measurements. After field collection, soils were transported cold (4 °C) to the laboratory at the University of California, Merced, and stored until processed (within 72 h of initial sampling). Field-moist soils were first sieved (2 mm mesh) and homogenized. Gravimetric water content was determined by oven-drying the sieved soil for 24 h at 105 °C. Oven-dried soils were analyzed for C and N (g kg<sup>-1</sup> soil) using an elemental combustion system (ECS 4010 CHNSO Analyzer, Costech Analytical Technologies, Valencia, California).

Ammonium and NO<sub>3</sub><sup>-</sup> concentrations were determined by extracting 5 g of field-moist soil with 25 mL of 2 M potassium chloride (KCl), filtered through Whatman No. 1 filter paper (preleached with deionized water), followed by flow injection analysis (QuikChem 8500, Lachat Instruments, Hach Company, Loveland, Colorado). Ammonium and NO<sub>3</sub><sup>-</sup> were determined by colorimetric methods on separate manifolds, the former using phenolate (method #12-107-06-1-B) and the latter using a cadmium-copper reduction column (method #12-107-04-1-B). The concentrations of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> were expressed as mg N kg<sup>-1</sup> dry soil.

#### DATA ANALYSES

Means and standard errors of soil VWC, temperature, CO<sub>2</sub> flux, CH<sub>4</sub> flux, and N<sub>2</sub>O flux were calculated for each date and distance along the hydrological gradient. A one-way analysis of variance (ANOVA) was used to test for differences between dates at an alpha level of 0.05 (JMP 8.0.2 software, SAS Institute, Cary, North Carolina). Linear regression was used to test relations between GHG fluxes, position in the meadow, soil microclimate, and chemistry.

Radiative forcing calculations were based on CH<sub>4</sub> and N<sub>2</sub>O being 25 and 298 times stronger per mole, respectively, than CO<sub>2</sub> as a greenhouse gas during the next 100 years (Forster et al., 2007). Hourly fluxes of CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O in each chamber were converted to g CO<sub>2</sub>-equivalents m<sup>-2</sup> d<sup>-1</sup>. In the cases of CH<sub>4</sub> and N<sub>2</sub>O consumption, values of CO<sub>2</sub>-equivalents were negative. We totaled the CO<sub>2</sub>-equivalents for each sampled chamber, and then averaged across all chambers to determine the mean rate of GHG emission from the meadow on each date. Because our intent was not to construct an annual GHG budget—and because we know little about

diurnal and weekly variation in GHG fluxes at this meadow—we refrained from temporal upscaling.

## Results

### SOIL MICROCLIMATE

Near-surface soils in the meadow were 2.2 °C warmer in July compared to September (Table 1). Soil VWC did not show a statistically significant difference from July to September, but VWC tended to decrease more in soils that were wetter in July. On both dates, ranges of soil VWC (~60%) and temperature (~10 °C) across the meadow were similar, and soils near the edge of the meadow were 23% drier (by volume) compared to the middle of the meadow (Fig. 1, part a). There was a negative correlation between soil temperature and VWC, particularly in September (Table 2). The distribution of soil VWC was normal in July and skewed in September (i.e., more locations with dry soil and fewer locations with wet soil). Soil gravimetric and volumetric water contents in September were positively correlated ( $P = 0.0007$ ;  $R^2_{\text{adj}} = 0.39$ ;  $\text{GWC} = 0.58\text{VWC} + 0.34$ ). The correlation may have been stronger if we would have included rock fragments >2 mm in the gravimetric calculation, or if we would have measured VWC in September at all 48 plots instead of 24 plots.

### CARBON DIOXIDE FLUX

Average CO<sub>2</sub> emission across all plots was three times greater in July than in September (Table 1). However, soil CO<sub>2</sub> emission did not vary significantly across the hydrological gradient (Fig. 1, part b). July CO<sub>2</sub> flux was not significantly explained by VWC or temperature, whereas September CO<sub>2</sub> flux showed a strong positive correlation with both VWC and temperature (Table 2). Plant

species richness was the best predictor of July CO<sub>2</sub> flux ( $F = 5.18$ ;  $P = 0.0039$  in one-way ANOVA; Fig. 2). September CO<sub>2</sub> flux was positively related to soil C and N concentration, but showed no correlation with extractable NH<sub>4</sub><sup>+</sup> or NO<sub>3</sub><sup>-</sup> concentrations (Table 2).

### METHANE FLUX

Net uptake of atmospheric CH<sub>4</sub> by soil predominated on both sampling dates (Table 1). Only 3 of the 48 plots (6%) showed net CH<sub>4</sub> emission in July, and only 1 of the 24 plots (4%) in September. The remaining plots showed net CH<sub>4</sub> uptake. Soil VWC and position on the hydrological gradient were the best predictors of CH<sub>4</sub> flux (Table 2; Fig. 1, part c). Drier soils near the edge of the meadow consumed roughly five times more CH<sub>4</sub> than wetter soils near the middle of the meadow. Methane flux was not correlated with soil temperature in July, but was positively correlated with temperature in September when VWC and temperature strongly covaried. There was no correlation between September CH<sub>4</sub> flux and soil concentrations of C, N, NH<sub>4</sub><sup>+</sup>, or NO<sub>3</sub><sup>-</sup> (Table 2).

### NITROUS OXIDE FLUX

Soil N<sub>2</sub>O fluxes did not vary significantly between July and September, and mean N<sub>2</sub>O uptake occurred on both dates (Table 1). In July, N<sub>2</sub>O uptake occurred more often in wetter soils near the middle of the meadow, while N<sub>2</sub>O emission occurred more often in drier soils near the edge of the meadow (Table 2, Fig. 1, part d). In September, N<sub>2</sub>O flux did not show this pattern of hydrological control. Soil N<sub>2</sub>O flux was also positively related to temperature in July but showed no relationship with temperature in September. There was no correlation between September N<sub>2</sub>O flux and soil concentrations of C, N, NH<sub>4</sub><sup>+</sup>, or NO<sub>3</sub><sup>-</sup> (Table 2).

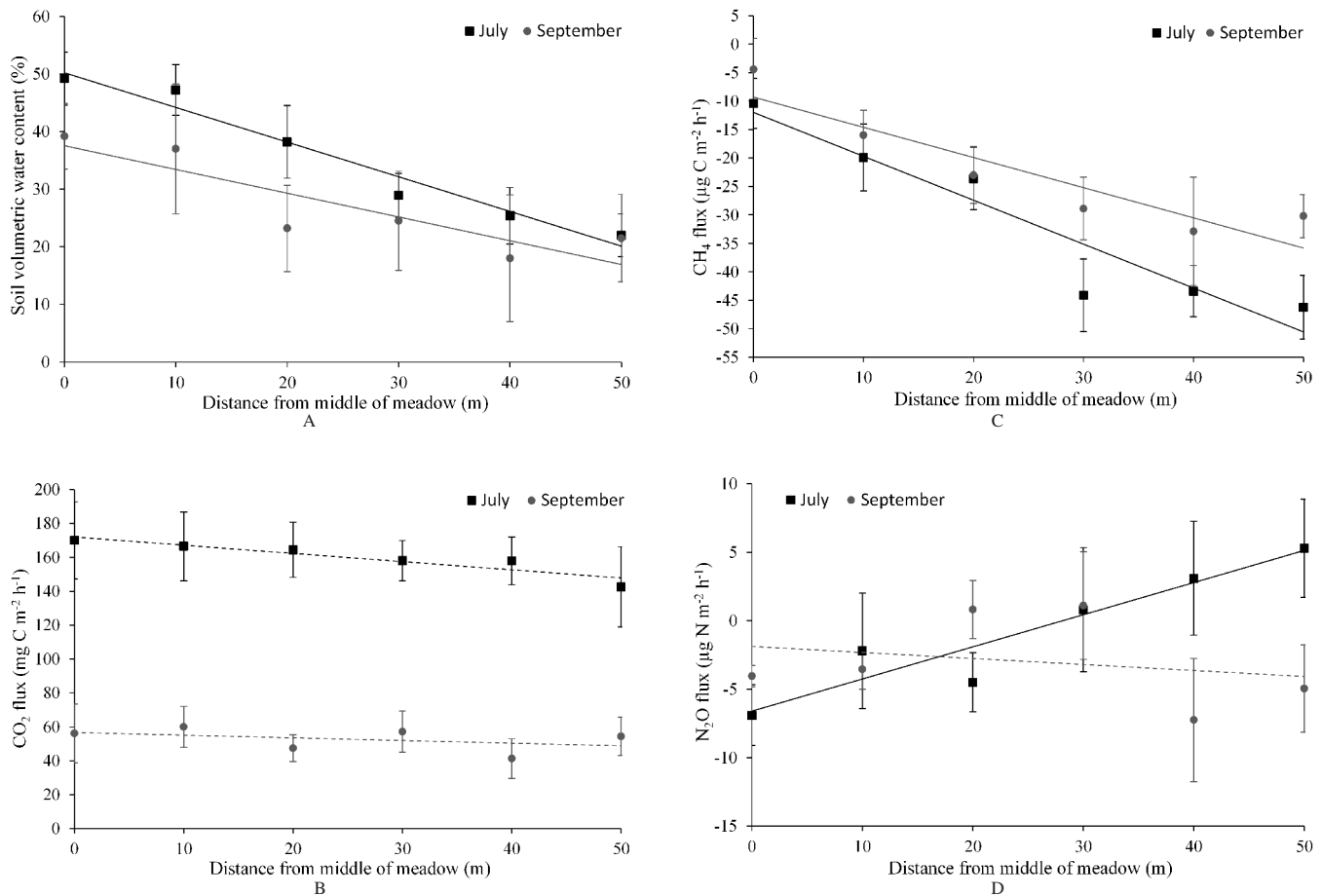
TABLE 1

Soil chemistry, microclimate, and midday fluxes of carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), and nitrous oxide (N<sub>2</sub>O) along a 50-m hydrological gradient in a Sierra Nevada subalpine meadow early (July) and late (September) in the growing season.

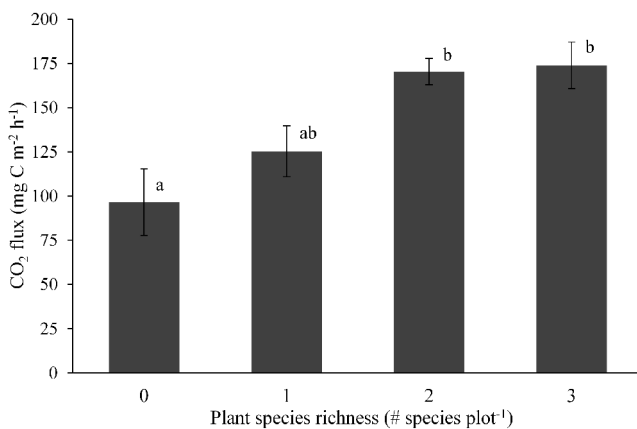
Measurement	Date	Mean	S.E.	C.V.	Range	F-ratio	P-value
Total carbon (g kg <sup>-1</sup> )	Sept	50.4	3.4	0.33	24–87	n.a.	n.a.
Total nitrogen (g kg <sup>-1</sup> )	Sept	3.1	0.2	0.32	1.6–6.0	n.a.	n.a.
Extractable ammonium (mg N kg <sup>-1</sup> )	Sept	2.11	0.39	0.91	0.51–8.37	n.a.	n.a.
Extractable nitrate (mg N kg <sup>-1</sup> )	Sept	0.40	0.15	1.82	<0.01–2.96	n.a.	n.a.
Volumetric water content (%)	July	35.2	2.4	0.47	7–69	3.46	0.067
	Sept	27.2	3.7	0.67	1–60	n.a.	n.a.
Temperature (°C)	July	15.5	0.4	0.16	12–22	14.47	0.0003*
	Sept	13.3	0.5	0.17	9–18	n.a.	n.a.
Carbon dioxide flux (mg C m <sup>-2</sup> h <sup>-1</sup> )	July	159.8	7.3	0.31	62–267	98.91	<0.0001*
	Sept	52.7	4.7	0.43	22–93	n.a.	n.a.
Methane flux (μg C m <sup>-2</sup> h <sup>-1</sup> )	July	–31.3	2.9	0.65	–78 to 9	3.54	0.064
	Sept	–22.6	3.0	0.64	–58 to 6	n.a.	n.a.
Nitrous oxide flux (μg N m <sup>-2</sup> h <sup>-1</sup> )	July	–0.6	1.6	17.95	–29 to 34	0.97	0.33
	Sept	–3.0	1.2	2.05	–20 to 12	n.a.	n.a.

Notes: Soil chemistry and volumetric water content were measured 0 to 12 cm deep, and soil temperature was measured 6 cm deep; positive gas fluxes indicate net emission from the soil to the atmosphere, and negative fluxes indicate net uptake from the atmosphere to the soil; S.E. is the standard error, and C.V. is the coefficient of variation (standard deviation divided by mean). \*Indicates significant difference between sampling dates in a one-way ANOVA at an alpha level of 0.05; n.a. indicates not applicable.





**FIGURE 1.** Variation in (a) soil moisture 0–12 cm deep and fluxes of (b) carbon dioxide ( $\text{CO}_2$ ), (c) methane ( $\text{CH}_4$ ), and (d) nitrous oxide ( $\text{N}_2\text{O}$ ) along a 50-m hydrological gradient in a Sierra Nevada subalpine meadow. The gradient extended from the wet middle (0 m) to dry edge (50 m) of the meadow. Soil moisture and gas fluxes (mean  $\pm$  standard error) were measured in July (black line;  $n = 8$ ) and September (gray line;  $n = 4$ ). The solid line indicates that the slope of the linear fit differed from zero at an alpha level of 0.05, and the dashed line indicates that the slope did not differ from zero. Negative fluxes indicate net uptake from the atmosphere to the soil, and positive fluxes indicate net emission from the soil to the atmosphere.



**FIGURE 2.** Variation in soil  $\text{CO}_2$  emission in July associated with plant species richness. Bars show means and standard errors. Letters indicate significant differences in Tukey's HSD test at an alpha level 0.05. There were 4, 7, 24, and 11 observations for plant species richness of 0, 1, 2, and 3, respectively.

#### RADIATIVE FORCING

An accounting of  $\text{CO}_2$ ,  $\text{CH}_4$ , and  $\text{N}_2\text{O}$  fluxes in terms of  $\text{CO}_2$ -equivalents showed that average GHG emission was three times greater in July than in September (Table 3). This difference was primarily due to reduced  $\text{CO}_2$  emission in September because  $\text{CO}_2$  was responsible for over 98.5% of net GHG emission. Net GHG emission did not vary significantly with soil VWC in July ( $F = 3.04$ ;  $P = 0.088$ ;  $R^2_{\text{adj}} = 0.04$ ;  $y = 0.067x + 11.69$ ), but net GHG emission and soil VWC were positively correlated in September ( $F = 26.18$ ;  $P < 0.0001$ ;  $R^2_{\text{adj}} = 0.52$ ;  $y = 0.082x + 2.35$ ; Fig. 3). Methane uptake contributed more to GHG emissions reduction in September than in July. Soil  $\text{N}_2\text{O}$  fluxes increased net GHG emission in July (by a maximum of 4%), but reduced GHG emission in September (by a maximum of 11%). The “cooling effect” of  $\text{CH}_4$  uptake increased with drying (linear fit:  $F = 48.02$ ;  $P < 0.0001$ ;  $R^2_{\text{adj}} = 0.40$ ;  $y = 0.014x - 0.77$ ) and was greatest in soils drier than 10% VWC (Fig. 4), or ~6% GWC.

TABLE 2

Relation between greenhouse gas fluxes (CO<sub>2</sub>, CH<sub>4</sub>, and N<sub>2</sub>O), soil microclimate, and chemistry in a subalpine meadow early (July) and late (September) in the growing season.

Predictor	Response variable	Date	ddf	Slope	R <sup>2</sup> adj	F-ratio	P-value
VWC (%)	Temperature	July	46	-0.05	0.11	7.10	0.011*
		Sept	22	-0.10	0.61	36.97	<0.0001*
	CO <sub>2</sub> flux	July	45	0.78	0.04	3.12	0.084
		Sept	22	0.93	0.52	26.32	<0.0001*
	CH <sub>4</sub> flux	Jul	46	0.92	0.56	59.63	<0.0001*
		Sept	22	0.51	0.39	15.57	0.0007*
	N <sub>2</sub> O flux	July	46	-0.21	0.08	5.28	0.026*
		Sept	22	-0.01	-0.04	0.04	0.84
Temperature (°C)	CO <sub>2</sub> flux	July	45	4.17	0.02	1.97	0.17
		Sept	22	-6.82	0.42	17.97	0.0003*
	CH <sub>4</sub> flux	July	46	-0.32	-0.02	0.07	0.80
		Sept	22	-4.07	0.38	14.98	0.0008*
	N <sub>2</sub> O flux	July	46	1.25	0.06	3.82	0.057
		Sept	22	0.28	-0.03	0.25	0.63
	CO <sub>2</sub> flux	Sept	22	0.58	0.14	4.83	0.039*
		Sept	22	0.28	0.07	2.61	0.12
Total C (g kg <sup>-1</sup> )	N <sub>2</sub> O flux	Sept	22	-0.02	-0.042	0.07	0.79
Total N (g kg <sup>-1</sup> )	CO <sub>2</sub> flux	Sept	22	9.06	0.12	4.16	0.054*
	CH <sub>4</sub> flux	Sept	22	4.26	0.05	2.11	0.16
	N <sub>2</sub> O flux	Sept	22	-0.38	-0.041	0.09	0.77
Ammonium (mg kg <sup>-1</sup> )	CO <sub>2</sub> flux	Sept	22	0.64	-0.042	0.06	0.80
	CH <sub>4</sub> flux	Sept	22	1.27	-0.016	0.63	0.44
	N <sub>2</sub> O flux	Sept	22	-0.48	-0.022	0.51	0.48
Nitrate (mg kg <sup>-1</sup> )	CO <sub>2</sub> flux	Sept	22	5.79	-0.0097	0.79	0.39
	CH <sub>4</sub> flux	Sept	22	3.38	-0.015	0.66	0.43
	N <sub>2</sub> O flux	Sept	22	0.99	-0.031	0.31	0.58

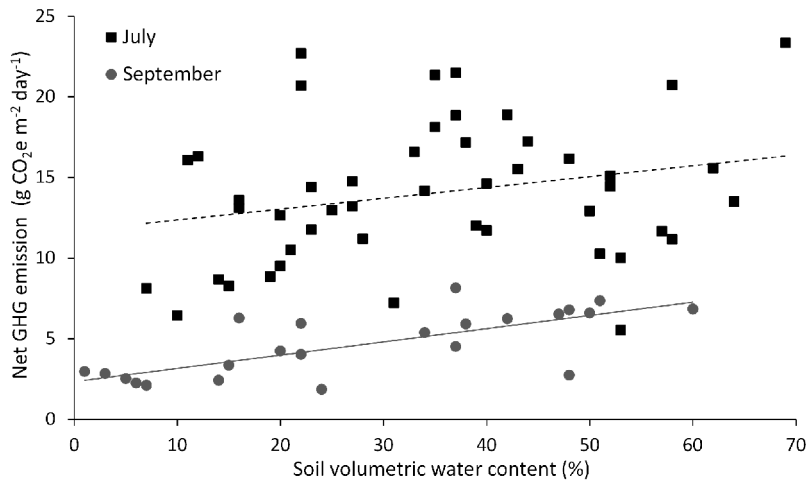
Notes: Soil volumetric water content (VWC) was measured 0 to 12 cm deep and temperature was measured 6 cm deep. R<sup>2</sup>adj is the adjusted coefficient of determination; ddf indicates the denominator degrees of freedom for the linear regression test; \*indicates significant linear regression between predictor (x) and response variable (y) at an alpha level of 0.05.

TABLE 3

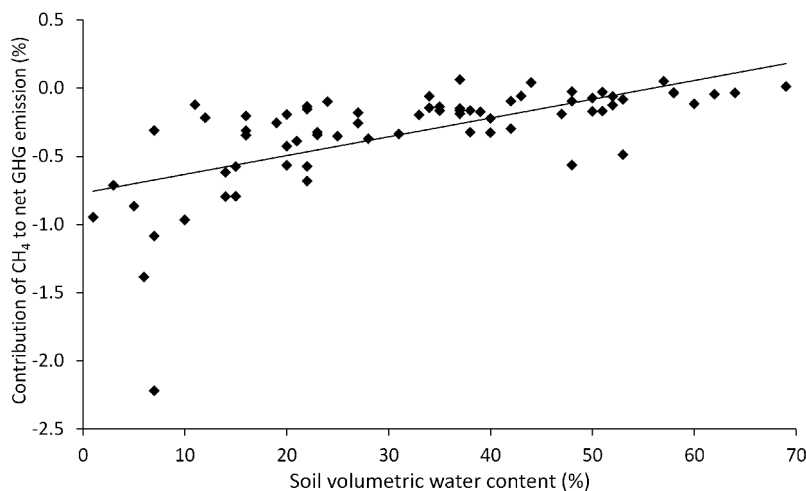
Net greenhouse gas (GHG) emission and relative contribution of methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) fluxes to radiative forcing in a subalpine meadow.

Metric	Date	Mean	S.E.	Range	F-ratio	P-value
Net GHG emission (g CO <sub>2</sub> e m <sup>-2</sup> d <sup>-1</sup> )	July	14.03	0.64	5.5–23.3	100.66	<0.0001*
	Sept	4.58	0.41	1.9–8.2		
CH <sub>4</sub> contribution to GHG emission (%)	July	-0.21	0.03	-1.0 to 0.1	15.64	0.0002*
	Sept	-0.55	0.11	-2.2 to 0.1		
N <sub>2</sub> O contribution to GHG emission (%)	July	0.11	0.16	-1.6 to 4.3	6.13	0.016*
	Sept	-0.96	0.52	-10.6 to 3.1		

Notes: Fluxes of CH<sub>4</sub> and N<sub>2</sub>O were transformed to CO<sub>2</sub> equivalents (CO<sub>2</sub>e) by multiplying by radiative forcing factors of 25 and 298, respectively; CO<sub>2</sub>e<sub>total</sub> per plot was averaged across all plots in the meadow to calculate net GHG emission for each date; the contribution of CH<sub>4</sub> per plot was calculated as: CO<sub>2</sub>e<sub>methane</sub>/CO<sub>2</sub>e<sub>total</sub> \* 100%; the contribution of N<sub>2</sub>O per plot was calculated as: CO<sub>2</sub>e<sub>nitrous oxide</sub>/CO<sub>2</sub>e<sub>total</sub> \* 100%; positive contribution indicates a warming effect and negative contribution indicates a cooling effect; \* indicates significant difference between sampling dates at an alpha level of 0.05.



**FIGURE 3.** Relation between soil volumetric water content and net greenhouse gas (GHG) emission in July (solid line) and September (dashed line). Solid line indicates that the slope of the linear regression was significantly different from zero at an alpha level of 0.05, and dashed line indicates that the slope was not significantly different from zero. Net GHG emission in each plot was calculated as the net flux of carbon dioxide equivalents ( $\text{CO}_2\text{e}$ ) based on the radiative forcing per mole of carbon dioxide (1), methane (25), and nitrous oxide (298).



**FIGURE 4.** Relation between soil volumetric water content and the contribution of methane ( $\text{CH}_4$ ) to net greenhouse gas (GHG) emission. The regression indicates a significant linear fit across sampling dates at an alpha level of 0.05. The contribution of  $\text{CH}_4$  to net GHG emission in each plot was calculated as the  $\text{CO}_2$ -equivalents consumed or produced by soil as  $\text{CH}_4$  ( $\text{CO}_2\text{e}_{\text{methane}}$ ) divided by the total soil GHG emission including  $\text{CO}_2$  and  $\text{N}_2\text{O}$  ( $\text{CO}_2\text{e}_{\text{total}}$ ), and then multiplied by 100%. Negative values indicate a decrease in  $\text{CO}_2\text{e}_{\text{total}}$  and a net cooling effect.

## Discussion

Our goal was to capture spatial variability of multiple GHG fluxes to infer their abiotic and biotic controls using a soil moisture gradient. Despite half as much water in surface soil at the edge of the meadow,  $\text{CO}_2$  emission showed no obvious spatial pattern across the hydrological gradient on either date. Soil moisture was less important than we expected in explaining  $\text{CO}_2$  fluxes. Soil  $\text{CO}_2$  emission varied more in time than in space, likely because later in the growing season there was reduced plant root respiration, greater microbial C limitation, and colder temperatures (Jiang et al., 2010). Early in the growing season, soil  $\text{CO}_2$  fluxes (but not  $\text{CH}_4$  or  $\text{N}_2\text{O}$  fluxes) were best explained by a positive correlation with plant species richness. The plots with no aboveground plant growth (i.e., richness = 0) emitted the least amount of  $\text{CO}_2$ . This suggests that the abundance and resource utilization of plants were linked to spatial patterns of soil  $\text{CO}_2$  emission. Root respiration, exudates, and priming of soil organic matter in the rhizosphere could drive this spatial pattern (Bird et al., 2011; Geng et al., 2012; Guenet et al., 2012). Drought conditions can increase the occurrence of bare ground in montane meadows (Debinski et al., 2010), and, in our study, bare ground was associated with roughly one-third less soil  $\text{CO}_2$  emission. Root respiration, therefore, perhaps accounted for a maximum of 30% of soil respiration.

It was not until later in the dry season that  $\text{CO}_2$  emission showed signs of water limitation. For example,  $\text{CO}_2$  emission and soil moisture showed a strong positive correlation in September (mean VWC = 27%) but not in July (mean VWC = 35%). However, the large seasonal reduction in  $\text{CO}_2$  emission even on the wet side of the hydrological gradient suggests that labile carbon was more limiting than water. And if microbial and plant respiration were water stressed in drier soils, then less  $\text{CO}_2$  production in shallow soil was apparently compensated by greater  $\text{CO}_2$  transport from deeper, wetter soil (Pacific et al., 2008). Whatever the mechanism, we found that topographic position within the meadow, and associated variation in near-surface soil moisture, had little influence on rates of  $\text{CO}_2$  emission during the growing season.

We also find it surprising that, at least on our sampling dates, the wet middle of the meadow rarely emitted  $\text{CH}_4$ . In contrast to a Rocky Mountain subalpine meadow (Mosier et al., 1993) and a lower-elevation Sierra Nevada wetland (Oates et al., 2008), the subalpine meadow that we studied emitted little  $\text{CH}_4$ , perhaps because of a lower water table (Smith et al., 2003) or the coarse-textured, well-drained soils in the High Sierra (USDA NRCS, 2007; Bales et al., 2011). It is also likely that we missed pulses of  $\text{CH}_4$  emission in the middle of the meadow during thawing and post-snowmelt flooding (Mosier et al., 1993). The edge of the meadow showed more  $\text{CH}_4$  uptake, supporting the negative relationship be-



tween soil moisture and CH<sub>4</sub> consumption in montane meadows (Mosier et al., 1993; Torn and Harte, 1996; Lin et al., 2009; Jiang et al., 2010). Drier soils transport more atmospheric oxygen and CH<sub>4</sub>, thus inhibiting methanogenesis and reducing diffusional limitation on methanotrophy (Conrad, 1996; Hanson and Hanson, 1996). Therefore, CH<sub>4</sub> fluxes varied more predictably than CO<sub>2</sub> and N<sub>2</sub>O fluxes, showing little temporal variation and a high degree of spatial organization according to soil moisture.

As the first measurements of field N<sub>2</sub>O fluxes in a high-elevation Sierra Nevada meadow, it surprised us that net N<sub>2</sub>O consumption was so prevalent. We expected wet soils to emit more N<sub>2</sub>O because of less oxygen and greater denitrification (Smith et al., 2003). Instead, it appears that nitrification was the main source of N<sub>2</sub>O (Firestone and Davidson, 1989; Stark et al., 2002), at least when surface soil was warm enough (i.e., July) and dry enough (i.e., edge of meadow). Drier conditions increase oxygen diffusion into the soil from the atmosphere and may prevent denitrifying microbes from reducing N<sub>2</sub>O to dinitrogen gas (N<sub>2</sub>), thus increasing N<sub>2</sub>O emission (Burgin and Groffman, 2012). Wetter conditions, on the other hand, can favor the reduction of N<sub>2</sub>O to N<sub>2</sub>, causing less N<sub>2</sub>O production (Avrahami and Bohannan, 2009) or net N<sub>2</sub>O consumption, especially when soil NO<sub>3</sub><sup>-</sup> concentration is sufficiently low (<1 mg N kg<sup>-1</sup>; Rosenkranz et al., 2005; Chapuis-Lardy et al., 2007; Wu et al., 2013). Observed rates of N<sub>2</sub>O uptake were greater than those found in other meadows (Mosier et al., 1993; Filippa et al., 2009; Jiang et al., 2010), and rates of N<sub>2</sub>O emission were an order of magnitude lower than other meadows (Filippa et al., 2009; Lin et al., 2009; Hu et al., 2010), but similar to a low-elevation Sierra Nevada wetland (Oates et al., 2008). Mosier et al. (1993) found the highest rates of N<sub>2</sub>O emission in a Rocky Mountain meadow 3 to 7 weeks after snowmelt, which is the time period when we first visited our site. However, the N<sub>2</sub>O pulse could have happened earlier; during spring thaw, for example (Christensen and Tiedje, 1990). There is evidence from a variety of Sierra Nevada ecosystems—including a wet meadow—that the largest N<sub>2</sub>O pulse from denitrification occurs during winter instead of summer (Walker et al., 1992). The Sierra Nevada meadow we studied supports this pattern because it was not a strong N<sub>2</sub>O source during the growing season, and it could perhaps switch from sink to source with future climate-induced soil drying.

Methane and N<sub>2</sub>O contributed most to the net GHG flux on the dry side of the hydrological gradient, not the wet side as predicted. Net GHG emission was foremost determined by CO<sub>2</sub>, but CH<sub>4</sub> and N<sub>2</sub>O were more important to account for in drier soils and later in the growing season after plant senescence. In terms of CO<sub>2</sub>-equivalents, CH<sub>4</sub> consumption in drier soils reduced GHG emission by up to 2%. This contribution of CH<sub>4</sub> uptake to the net GHG flux was greater than found in a Tibetan Plateau meadow (~0.2%), despite similar ranges of soil moisture and temperature (Jiang et al., 2010). Soil N<sub>2</sub>O production at our site accounted for up to 4% of GHG emission in relatively warm (July) and dry soils (edge of meadow). In colder (September) and wetter soils (middle of meadow), however, N<sub>2</sub>O consumption reduced net GHG emission by up to 11%. Although the spatially averaged N<sub>2</sub>O flux for July showed consumption, the negative correlation between CO<sub>2</sub> emission and N<sub>2</sub>O emission ( $P = 0.0016$ ;  $R^2_{\text{adj}} = 0.18$ ;  $N = 48$ ) probably explains why N<sub>2</sub>O showed an overall positive—albeit small—contribution to radiative forcing. Because lower CO<sub>2</sub> emission indicates bare ground, perhaps less N uptake by plants resulted in more N available for N<sub>2</sub>O emission. Unfortunately, we did not measure soil N concentrations earlier in the growing season. Nevertheless, the warming effect of N<sub>2</sub>O emission at the edge of the meadow slightly

outweighed the cooling effect at the middle of the meadow. These results demonstrate the potential for hydrological changes in high-elevation meadows to impact both the magnitude and direction of the effects of non-CO<sub>2</sub> GHGs on net radiative forcing.

Because of the low sampling frequency (twice during the snow-free season), we had no intention of upscaling to an annual GHG budget, or upscaling beyond this single meadow. We no doubt missed important GHG emissions during freeze-thaw and flooding events in the winter and spring before we could access the site (Teepe et al., 2001; Goldberg et al., 2008; Liptzin et al., 2009). Another limitation of our study is that soil chemistry was measured only on one date; thus we cannot determine the relative importance of hydrology vs. chemistry in explaining GHG fluxes across dates. Our intention—rather—was to use space as a surrogate for time to indicate what happens when the soil dries during the summer and what could happen when the climate dries in the future.

In conclusion, we found no evidence that the wet middle of a montane meadow was a hotspot of GHG emission during the snow-free season compared to the drier edges. Soil CO<sub>2</sub> and net GHG emission varied little across the hydrological gradient. However, soil drying enhanced CH<sub>4</sub> uptake and N<sub>2</sub>O emission, at least in the short-term, which highlights the importance of quantifying the balance of non-CO<sub>2</sub> gases for GHG budgets in heterogeneous montane landscapes. Other factors could also interact with hydrological changes in high-elevation meadows to impact GHG fluxes. For example, recreational packstock use and livestock grazing, which are common in Sierra Nevada meadows, can compact soil (i.e., less gas diffusivity and water-filled pore space), increase coverage of bare ground, and alter C and N inputs to soil (Kosco and Bartolome, 1981; McClaran, 1989; Cole et al., 2004), perhaps creating a more heterogeneous pattern of GHG emission with more hotspots. Furthermore, shifts in meadow plant community composition associated with climate change, exotic species, and conifer encroachment could impact C and N inputs, microclimate (Dyer and Moffett, 1999; Haugo and Halpern, 2007; Debinski et al., 2010; Zald et al., 2012), and thus GHG fluxes. Amidst all these changes, hydrological gradients in montane meadows can serve as the context for spatial upscaling and an improved understanding of the underlying mechanisms of GHG emissions.

## Acknowledgments

We thank NSF-supported REU student Alison Nill for her essential help with site selection, field logistics, field measurements, and data analysis. We thank Elizabeth Ballenger and Eric Berlow for sharing important data regarding site selection. We thank Emma McCorkle, Erin Stacy, and Steven Lee for their help with field measurements, laboratory measurements, and data analysis. We thank Carol, Kira, and Lukas Hart for their help with September gas sampling. We thank Sally Thompson and Vincent Pacific for ideas on interpreting data. We also thank the Resources Management and Science Division at Yosemite National Park and the National Park Service for providing the venue and logistical support for this project. This research was financially supported by the National Science Foundation's Research Experience for Undergraduates Program (Award ID-0649092) and the Kearney Foundation of Soil Science (Kearney-2009.023).

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MS accepted January 2014